

REVIEW

Spider silk: a brief review and prospectus on research linking biomechanics and ecology in draglines and orb webs

Todd A. Blackledge: Department of Biology and Integrated Bioscience Program, The University of Akron, Akron, OH 44325-3908 USA. E-mail: blackledge@uakron.edu

Abstract. Spiders construct a wide variety of silk structures, ranging from draglines to prey capture webs. Spider silks rank among the toughest materials known to science, and these material properties are critical for understanding how silk structures, such as webs, function. However, the mechanics of spider silk are often ignored in the study of webs. This review aims to show how the material properties of silk proteins, the structural properties of silk threads, and the architectures of webs ultimately interact to determine the function of orb webs during prey capture. I first provide a brief introduction into spider silk and how to characterize its material and structural properties. I then examine the function of draglines as “lifelines” to provide a well-understood example of the interaction of material and structural properties in silk function. Next, I examine how orb webs function in prey capture by first intercepting insects, then stopping their kinetic energy of flight, and finally retaining the insects long enough to be subdued by spiders. I show how variation in the material and structural properties of silk acts synergistically to facilitate the stopping and retention potentials of orb webs, and why this can occur in opposition to how orb webs intercept prey. Finally, I summarize why information on the material properties and structures of silk threads needs to be better incorporated into future investigations of spider webs in general.

Keywords: Biomechanics, flagelliform, major ampullate, orb web, prey capture, protein, spider silk

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1. INTRODUCTION

Silks are critical for the survival and success of the world’s more than 41,000 species of spiders (Platnick 2011). The purpose of this review is first to provide a brief introduction to silk to serve as a primer for biologists studying spiders in the field, and then to examine some of the critical questions about spider ecology and evolution that can only be addressed by incorporating an improved understanding of silk production and mechanics. I first explore how silk mechanics relates to the relatively simple function of dragline “lifelines” as a well-understood example. I then focus specifically on the modern orb web and the silks used to produce it because orb-weaving spiders are the model system for studies on spider silk, and the functions of orb webs are much better investigated by biologists in the field compared to any other web type. I also focus primarily on the most recent research because historical perspectives are already available for spiders’ silks (Gosline et al. 1986; Craig 1997; Hayashi et al. 1999; Vollrath 1999; Hu

et al. 2006; Vollrath & Porter 2006; Eisoldt et al. 2011), web ecology and evolution (Shear 1986; Eberhard 1990; Wise 1993), and, more recently, the interface between webs and silk (Craig 2003; Vollrath & Selden 2007; Brunetta and Craig 2010; Blackledge et al. 2011; Harmer et al. 2011).

All spiders produce silk throughout their lives, and most are capable of spinning multiple types of silk threads. Spider silk threads are extruded from discrete glands through individual spigots located on their abdominal spinnerets. The silk threads are assembled nearly instantaneously from liquid feedstocks, or “dopes”, of protein at ambient temperatures and without caustic chemicals (Eisoldt et al. 2011). Spider silks rank among the toughest energy absorbing materials known (Vollrath & Porter 2009), requiring up to 7–10 times more energy to fracture than an equivalent volume of synthetic Kevlar (Agnarsson et al. 2010). The substantial interest in spider silk is therefore primarily motivated by the potential to exploit spider silks’ incredible mechanical properties for applications

ranging from high performance textiles to medical devices (Altman et al. 2003; Kluge et al. 2008). As a result, we now have a fairly robust set of hypotheses to explain the process of fiber assembly and the molecular basis behind the high performance for at least one type of silk – the major ampullate dragline silk used by orb-weaving spiders as the frameworks of their webs (Vollrath & Porter 2009; Eisoldt et al. 2011). Understanding of the silk gene family that encodes most spider silk proteins, commonly termed “spidroins” because they are spider-specific and fibrous, has expanded substantively in recent years (Gatesy et al. 2001; Ayoub et al. 2007; Garb et al. 2010). Yet, research linking silk to the function of structures built by spiders – particularly prey capture webs, draglines, and egg sacs is generally lacking (e.g., Harmer et al. 2011).

2. SPIDER SILK STRUCTURE AND PRODUCTION

Silk production is broadly distributed among arthropods, evolving independently in several orders of insects, crustaceans and arachnids (Craig 1997). Yet, silk is only loosely defined as semi-crystalline fibrous proteins that are extruded external to an organism’s body. However, the mechanical and biochemical diversity of silks is staggering. Spiders are unique in their reliance on silk throughout their lives, their diverse uses of silk, and their production of toolkits of as many as seven or eight different types of silks, each of which has a unique chemical composition and comes from its own discrete gland(s) and associated spigot(s) (Guerette et al. 1996; Blackledge & Hayashi 2006a; Vollrath & Porter 2006; Dicko et al. 2008). Most spider silk proteins are encoded by members of the spidroin gene family, whose evolutionary history is characterized by bouts of gene duplication followed by strong diversification (Gatesy et al. 2001; Gaines & Marcotte 2008; Garb et al. 2010). However, some recently discovered silk proteins are difficult to homologize to the known spider silk gene family – in particular some of the proteins found in the piriform attachments that cement threads together (Hu et al. 2007).

Various spider silks can match the tensile strength of steel (major ampullate silk), absorb more kinetic energy before rupturing than Kevlar (many types of silks), or reversibly stretch almost as far as rubber (flagelliform silk; Blackledge & Hayashi 2006a). These remarkable properties are explained by both the amino acid sequences of spider silk proteins and the way that those proteins are assembled into fibers. Silk is spun from liquid dope through spigots on the spinnerets of spiders (Fig. 1A). The dope assembles into a solid fiber through a phase shift in the structural arrangement of the spidroins, which interlocks the individual molecules, rather than simply “drying out”. Thus, the conditions under which the liquid dope is spun can dramatically influence the molecular structure, and hence performance, of the resulting fibers, even for the same starting dope. While the relative importance of protein composition vs. spinning effects for spider silk properties is sometimes debated in specific contexts, there is a general consensus that both matter. Importantly, this means that plasticity in silk properties could evolve through either mechanism (Tso et al. 2007; Boutry & Blackledge 2008; Boutry & Blackledge 2009).

2.1. Protein composition.—Orb spiders famously produce seven different types of silk fibers and glues that are

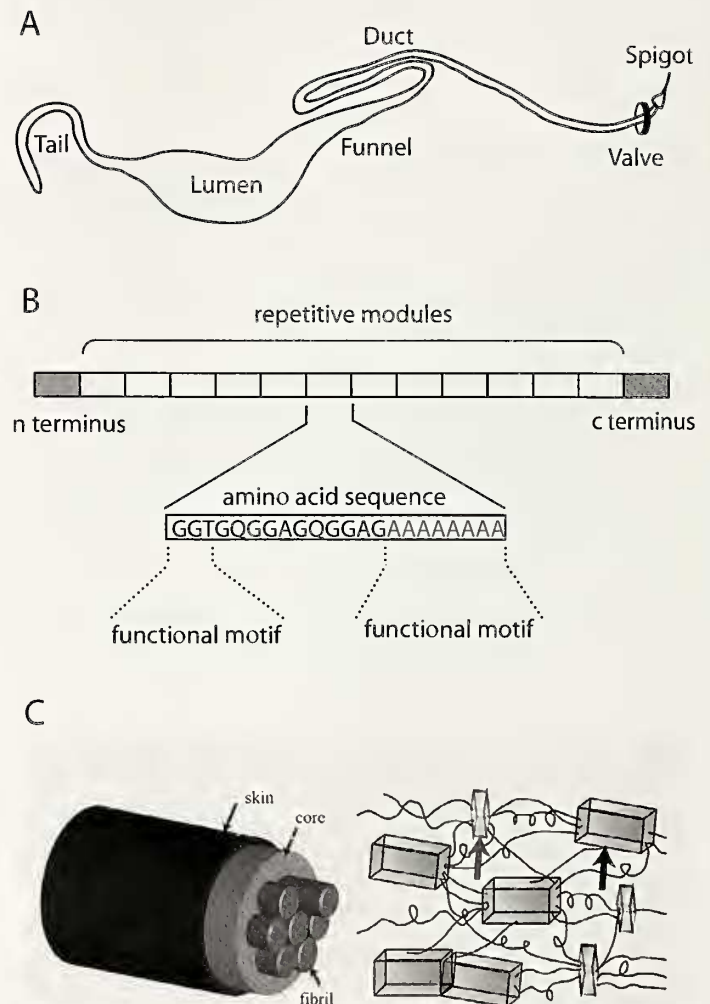


Figure 1.—Production and structure of major ampullate silk. (A) Silk proteins are initially secreted in the tail of the major ampullate silk gland and stored as a liquid dope in the lumen. Shear forces, water uptake, and ion exchange in the funnel and duct cause a phase shift so that new secondary structures form in the spidroins. These structures interlink individual molecules, causing the silk to solidify. A muscled valve provides a final draw down as the fiber exits the spigot, influencing the alignment of the molecules along the axis. From Blackledge et al. 2011. (B) Silk proteins largely consist of repeated sequences of amino acids. Motifs are short sequences of amino acids that are hypothesized to form specific secondary structures in silk such as β -sheets or β -spirals. Several of these motifs are arrayed sequentially to form a repetitive module. Several repetitive modules are themselves arrayed sequentially to form the bulk of the spidroin. This repetitive region is flanked on both ends by ~ 200 amino acid long terminal regions. From Blackledge et al. 2011. (C) Basic structure of major ampullate silk. A single thread consists of a thin skin of lipids and glycoproteins that surround a core that might show hierarchical layers of organization. Here, the core consists of multiple fibrils. The fibrils consist of a mix of highly crystalline domains embedded in an amorphous matrix. Two levels of crystalline domains are shown here. From Eisoldt et al. 2011.

distinguished by the spigots from which they emerge (Coddington 1989), their mechanical properties (Blackledge & Hayashi 2006a), and their amino acid sequences (Guerette et al. 1996). The general structure of most spidroins consists primarily of a central region of repetitive modules (also called ensemble repeats), with 10–100 of these modules making up

the core region, and flanking N (amino) and C (carboxyl)-termini that are ~100–200 amino acids in length (Fig. 1B; Ayoub et al. 2007). The N and C termini are strongly conserved across different types of silks, both within and among species (Gatesy et al. 2001; Garb et al. 2010; Hagn et al. 2010). In contrast, the repetitive modules are often incredibly homogeneous within a particular protein, but highly divergent among silk types (Gatesy et al. 2001). The repetitive modules range from ~50–200 amino acids in length, and short runs of specific amino acids are hypothesized to fold into various secondary structures that influence the performance of the resulting fiber (Guerette et al. 1996; Hayashi et al. 1999).

The semi-crystalline nature of spider silk threads means that much of the repetitive regions of the spidroins are confined in highly organized secondary structures (Fig. 1C). For instance, in the major ampullate silk that comprises draglines and the dry silk frames of orb webs, long repeats of alanine or glycine-alanine fold into β -sheets that are hypothesized to stack together and form nanocrystals that interlock individual molecules (Termonia 1994; Grubb & Jelinski 1997; van Beek et al. 2002; Jenkins et al. 2010). The remarkable strength of these crystals is derived in part from hydrophobic interactions that confine hydrogen bonds within the crystal lattice. This confinement is hypothesized to be a key element in explaining how relatively weak hydrogen bonds make for strong silk (Keten et al. 2010). Glycine-rich “amorphous regions” of the spidroins interconnect the crystal forming domains, and here the individual molecules are less confined spatially, often forming loose helices (Simmons et al. 1996; Lefevre et al. 2007). Hydrogen bonding and physical entanglement provide strength and rigidity to the amorphous region, but are easily disrupted as silk is stretched. The end result, at the macroscale, is a fiber that is both strong and stretchy. In stretchier silks, like the flagelliform silk that forms the inner axial fiber of the capture silk in orb webs, the crystal-forming domains are replaced by sequences of amino acids that form β -spirals when proline kinks the amino acid chains (Becker et al. 2003). This greatly increases the overall mobility of the molecules and plays a significant role in the function of orb webs (see Section 3.3). General summaries of the various secondary structures occurring in different types of spider silks are readily available (e.g., Hayashi et al. 1999; Blackledge & Hayashi 2006a; Hu et al. 2006).

Silk threads likely include additional levels of structural organization (Fig. 1C; Sponner et al. 2007). For instance, major ampullate threads are surrounded by sheaths of glycoproteins and lipids (Frische et al. 1998; Augsten et al. 2000). Internally, the core of the thread may be arranged into nanofibrils or contain elongate cavities that may distribute energy and help to prevent crack propagation as energy is propagated longitudinally rather than in the plane of the crack (Li et al. 1994; Frische et al. 1998). The sheath is particularly interesting from a functional standpoint because many spiders can use silk in chemotactile communication (Clark & Jackson 1995; Persons et al. 2002; Gaskett 2007) and the lipids in the sheath are a likely source of these compounds (Schulz 2001).

2.2. Spinning effects.—Silk fibers are assembled from liquid dopes through a process that is reasonably well characterized for the major ampullate dragline silk from *Nephila* and *Araneus*. But, almost nothing is known about the production

of other types of silks (both within these two “model genera” and among other species). Good reviews on the topic are available, although some of the details are controversial (e.g., Knight et al. 2000; Vollrath & Knight 2001; Chen et al. 2006; Eisoldt et al. 2011). I briefly review silk processing because of its importance in ultimately determining silk properties.

Liquid silk is stored within the lumen of the gland at high concentration, up to 50% wt/vol (Vollrath & Knight 2001), with fibroins packed together in micelles that isolate the central repetitive modules of the fibroins in the interior (Jin & Kaplan 2003; Hagn et al. 2010). Solidification of the fiber occurs when the structure of these micelles is disrupted such that the termini can dimerize, and the crystal forming motifs in the central repetitive regions of the proteins are no longer isolated so that their hydrophobic nature instead leads to the formation of β -sheets that stack together and interlock individual fibroins (Knight & Vollrath 1999; Askarieh et al. 2010; Hagn et al. 2010). This process is mediated by a combination of water resorption, ion exchange, drop in pH, and shear flow as the dope passes through an elongated “S”-shaped duct (Dicko et al. 2004; Lefevre et al. 2008; Askarieh et al. 2010). A final draw-down of now solid, but still wet fiber occurs at the narrow distal end of the duct, which is mediated in part by a muscled valve in orb spiders (Vollrath & Knight 1999; Ortlepp & Gosline 2004; Pérez-Rigueiro et al. 2005).

Spiders can control the amount of force applied to silk during the final drawn-down (Ortlepp & Gosline 2004; Pérez-Rigueiro et al. 2005). This affects the degree to which spidroins are oriented along the axis of the silk thread and therefore ultimately how stiff and extensible silk threads can be. For instance, the material properties of major ampullate silk can vary almost 50% under different spinning conditions, even within individual spiders (Madsen et al. 1999; Pérez-Rigueiro et al. 2005; Boutry et al. 2011). Thus, the physical processing of the silk dope within the spinnerets of spiders plays a critical role in determining the final structure, and hence also the function, of silk threads (Fig. 1A).

2.3. Supercontraction.—The alignment of the amorphous regions of spidroins along the axis of major ampullate silk fibers is maintained by hydrogen bonding. Thus, the molecular orientation is highly responsive to the environment, particularly to humidity (Vollrath & Porter 2006; Holland et al. 2008; Savage & Gosline 2008; Creager et al. 2010). Supercontraction occurs when water infiltrates silk threads and disrupts hydrogen bonding, thereby mobilizing the spidroins and allowing them to move to a more disordered state (Jelinski et al. 1999; Yang et al. 2000; Eles & Michal 2004). The process is driven by increases in entropy, and the rearrangement of silk molecules occurs quite rapidly. Supercontraction can ultimately cause silk to shrink by up to 50% of its length or to generate substantial forces in confined threads (Work 1981; Boutry & Blackledge 2010). Once a thread has shrunk to its maximally contracted state, it can no longer supercontract unless external forces are applied (Blackledge et al. 2009a), although the silk continues to show a cyclic swelling and contraction that has been implicated for biomimetics (Agnarsson et al. 2009).

The functional implications of supercontraction for webs is debated (e.g., Bell et al. 2002 versus Savage et al. 2004), but remains to be tested in whole orb webs, leaving the potential

“adaptive” value of supercontraction controversial. However, supercontraction was recently hypothesized to provide spiders with a mechanism to control the overall alignment of molecules within silk during the spinning process (Guinea et al. 2005; Liu et al. 2005). Under this scenario, any effect of supercontraction on web function would likely be a byproduct of supercontraction’s critical role in silk production. Silk threads are still wet during the final draw-down phase at the end of the spinning duct such that they are effectively already supercontracted so that the amorphous fraction of the silk is still relatively mobile. Spiders can therefore control the overall alignment of the amorphous fraction and how the nanocrystals are packed within it by increasing or decreasing the shear forces applied to the fiber as it exits the spinning duct (Pérez-Rigueiro et al. 2005). Variation in the molecular alignment might therefore account for the high degree of plasticity in mechanical properties that can be exhibited by a spider under different spinning conditions.

3. MECHANICAL FUNCTION OF SILK

The mechanical properties of silk were once challenging to measure due to the small diameters of silk threads, but technology has advanced such that the properties of silk threads as thin as ~300–500 nm are now commonly characterized for studies ranging in focus from phylogenetic variation to phenotypic plasticity to biomimetics. However, data on silk mechanics are still typically lacking from studies focusing on spider web ecology per se. The goal here is to summarize the essentials of the mechanical analysis of silk and some of the implications of variation in the material and structural properties for two common silk devices – draglines and orb webs (Fig. 2).

Spider silks are viscoelastic polymers that change their material properties as they are stretched. Therefore, variation in how silks perform when they are initially strained, even small amounts, can be as interesting and important as their behaviors at failure. Most mechanical analyses of silk focus on the stress-strain behavior of fibers because these values are normalized to the dimensions of the sample being tested, which facilitates comparison across different lengths or thicknesses of materials (Fig. 2A). These “material properties” then interact with the “structural properties” (e.g., thickness, length, number of fibers, etc.) to determine the functional properties of devices made from silk, such as how much force a web can sustain or how far it will stretch (Fig. 3; see below).

Stress measures the force generated within a fiber divided by cross-sectional area, while strain measures the ratio of the current to original length of a fiber. Two different methods of calculating stress and strain are common in the silk literature. “Engineering” values are normalized to the original specimen before it was stretched such that engineering stress (σ) is calculated as:

$$\sigma = \frac{F}{A}$$

where F is the applied force and A is the cross-sectional area. Engineering strain (ϵ) is calculated as:

$$\epsilon = \frac{\Delta l}{l_0}$$

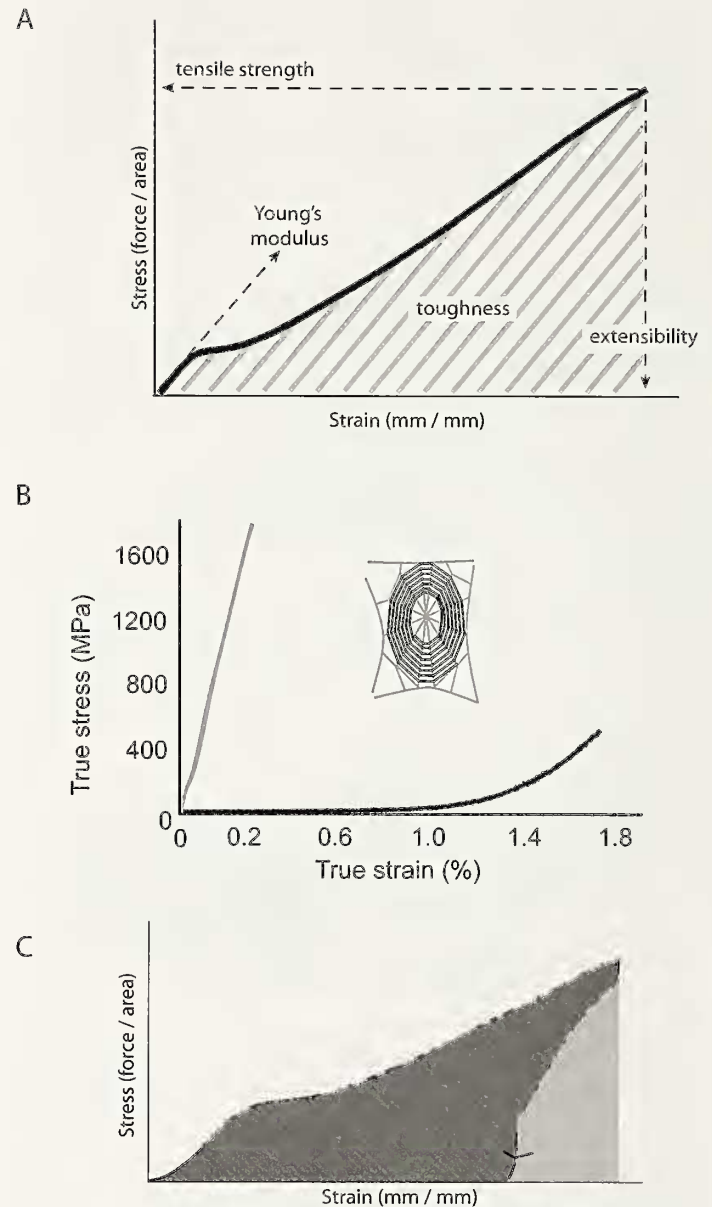


Figure 2.—Material properties of spider silk. (A) Stress-strain test of silk showing four of the most commonly measured material properties. See text for explanation. From Blackledge et al. 2011. (B) Comparison of the material properties of the two fibrous silk constituents of orb webs. The dry major ampullate silk framework (gray) has high tensile strength and stiffness. The wet flagelliform silk core of the capture spiral (black) is orders of magnitude more compliant and extensible. Both silks achieve relatively similar toughness. From Blackledge and Hayashi 2006b. (C) Hysteresis testing of silk. Silk is initially stretched (solid line) and then allowed to relax (dotted line). Energy damping is the proportion of the work performed to stretch a thread (total gray area) to that lost as heat (darker gray). If energy damping was 0%, then the material was perfectly elastic and the dotted line would mimic the original stress-strain test. Major ampullate silk typically has energy damping of ~60%. From Kelly et al. 2011.

where Δl is extension of the specimen and l_0 is the original length. In contrast, “true” values are normalized to the instantaneous dimensions of the specimen. For true stress, the instantaneous cross-sectional area A_i is substituted for A and

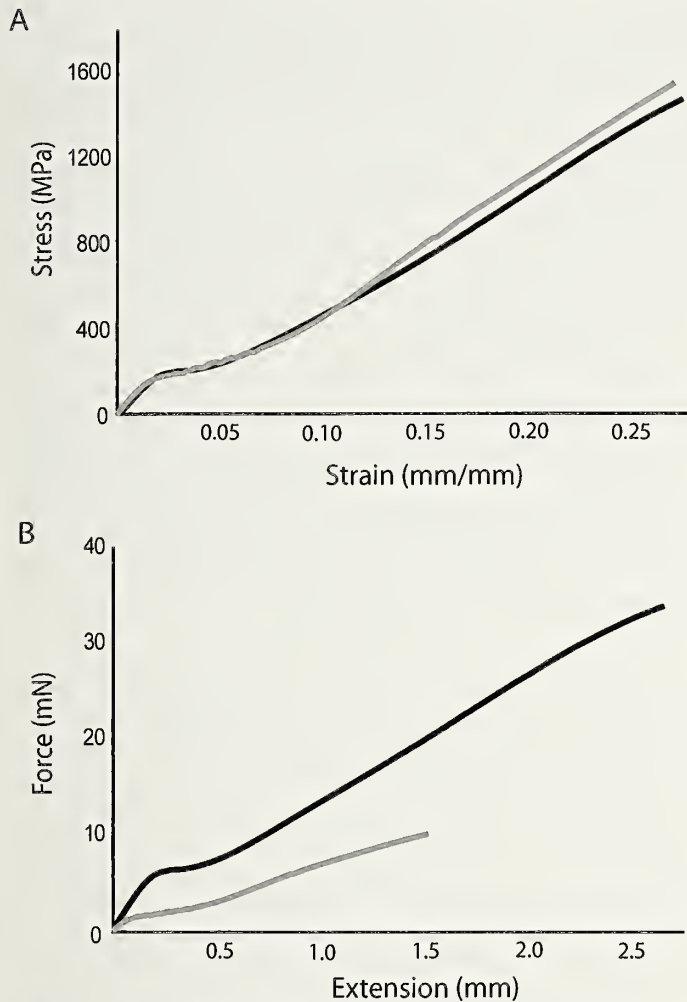


Figure 3.—Material versus mechanical performance of silk. (A) Material properties, such as stress and strain, express performance independent of the dimensionality of a sample to facilitate comparison among samples. Both a thicker, longer sample (black) and a thinner, shorter sample (gray) of the same type of major ampullate silk break at similar stress and strain. (B) However, the actual performance of silk structures also depends on their dimensions, so that it takes substantially more force to break a thicker silk thread (black) compared to the thinner silk (gray). Thus, both the material and structural properties of silk threads need to be considered because natural selection is expected to act upon the performance of structures per se.

is calculated assuming that the thread maintains a constant volume as it stretched. For true strain, the instantaneous length l_i is substituted for l .

These two methods diverge substantially for stretchy materials like spider silk. For instance, a 1-cm-long sample of capture spiral from an orb web could easily stretch 5 additional cm before breaking, which gives an engineering strain of 5 but a true strain of only 1.8 (if that thread broke at engineering stress of 200 MPa then its true breaking stress would be 1200 MPa!). Thus, it is always critical to identify how a given researcher calculates material properties when comparing across studies! Fortunately these measures are easily inter-converted where true stress (σ_t) is calculated as

$$\sigma_t = \sigma(1 + \epsilon)$$

and true strain (ϵ_t) is calculated as

$$\epsilon_t = \log_e(1 + \epsilon)$$

Much current research reports true stress and true strain for spider silks. Five aspects of material performance are typically calculated, as summarized in Figure 2A. Tensile strength (also called ultimate strength) and extensibility are simply the stress and strain at which a thread breaks, while the other measures merit further explanation. Young's modulus characterizes the initial stiffness of material, when minor deformations are highly reversible. Stiffness is calculated simply as the slope of the stress-strain curve. The yield point represents a transition in the behavior of the viscoelastic silk when the molecules begin to flow. This point represents a permanent change in the performance of the silk. Finally, the area under the stress-strain curve measures the toughness of the silk (also called work of extension), and it is the total work necessary to stretch a given volume of silk thread to failure. Toughness is where spider silk really excels. For instance, the tensile strength of dragline silk is only about half that of Kevlar but dragline silk's toughness is about five times greater, with Darwin's bark spider producing silk up to an impressive ten times greater (Agnarsson et al. 2010).

Many spider silks exhibit remarkably high hysteresis. Also called energy damping, hysteresis measures the capacity of a material to transfer kinetic energy to heat as it is deformed rather than storing that energy internally. Hysteresis is calculated simply as the difference in the loading versus unloading energy of a material (Fig. 2C). Major ampullate silk converts about 60% of loading energy to heat as it is stretched, and this amount is relatively conserved phylogenetically, at least among orb spiders where it has been investigated (Kelly et al. 2011). High hysteresis is critical for materials that must withstand high-energy impacts without storing that energy and returning it to the system. Flagelliform silk also has notably high hysteresis, but has to be stretched substantially before hysteresis becomes measureable. Thus, even when stretched to 20%, flagelliform silk acts more like a rubber band, rather than deforming plastically like the permanent thinning that occurs when pulling on a metal wire.

The above values are often called "material properties", but the performance of any silk thread also depends upon its "structural properties", such as thickness and length. By analogy, if you need a stronger rope to support a certain large weight, then you have two choices – you can trade your weaker cotton rope for a material like nylon, which has a higher tensile strength, or you can just get a thicker cotton rope; this is why both material and structural properties need to be considered to understand how webs function. It also leads to the really interesting evolutionary question: how do spiders meet the challenges of web performance in terms of stopping and retaining prey? Are there tradeoffs between structural and material properties? Or, do both evolve in a concerted fashion? These questions are particularly important because the mechanisms by which a spider could alter a web's performance through structural changes in silk lines are often much more apparent than those that could alter material properties. For instance, several species of orb spiders maintain a relatively constant safety factor for their draglines that drops only slightly over their lifetime not by improving

the tensile properties of silk as they grow in size, but simply by spinning thicker threads (Osaki 1996; Osaki 1999; Ortlepp & Gosline 2008). And, cobweb spiders adjust thread diameter when fed “high” versus “low” energy prey (Boutry & Blackledge 2008). On the other hand, several studies indicate that diet can influence the chemical composition of major ampullate silk (Craig et al. 2000; Tso et al. 2005; Guehrs et al. 2008) or aggregate glues (Higgins & Rankin 1999; Townley et al. 2006), although links to variation in mechanical performance of silk are rarely made (but see Tso et al. 2007).

4. SILK “LIFELINES”

Silk plays a fundamental role in how spiders move through the environment – from draglines to bridge lines to ballooning threads. The material and structural properties of silks are critical for each of these functions, and investigations are beginning to unravel how silk functions in both ballooning (Bell et al. 2005; Reynolds et al. 2006) and bridging (Rodríguez-Girones et al. 2010). Draglines present one of the most easily understood structure-function relationships in silk when they act as lifelines for falling or abseiling spiders. Thus, I use draglines to illustrate some of the key concepts to focus upon when considering how silk functions in more complex silk structures such as prey capture webs.

Spiders increase in mass by several orders of magnitude as they mature, and the forces a dragline sustains when stopping a falling spider scale similarly. A safety coefficient describes the degree to which the performance of structures can exceed their functional criteria – for instance, the amount of stress required to fracture a dragline relative to the stress generated by stopping a falling spider (Osaki 1999; Ortlepp & Gosline 2008). *Nephila* maintain a relatively static safety coefficient that decreases from about 3 to 2 as they mature simply by spinning thicker threads (Osaki 2003). In contrast, the safety factor for *Araneus diadematus* draglines decreases through ontogeny to the point where they cannot sustain a falling spider (Ortlepp & Gosline 2008). These spiders survive falls by actively releasing extra silk so that they decelerate gradually and some of the work necessary to stop their fall is performed by the muscled valve in the spinning duct itself (Ortlepp & Gosline 2008). Interestingly, major ampullate silk also has a shape memory – high energy damping under torsional (twisting) loading reduces the tendency of silk threads to spin as spiders hang from their draglines when falling or abseiling (Emile et al. 2006; Emile et al. 2007).

Some orb spiders also vary the mechanical performance of draglines based upon what might be an assessment of the risk of falling. Heavier *Argiope trifasciata* spin proportionally thicker draglines when climbing up surfaces compared to smaller individuals, such that spider mass is just less than the force necessary to cause a silk fiber to yield (Garrido et al. 2002). This means that a spider simply hanging from a silk dragline does not cause it to yield, which would cause permanent plastic deformation of the silk molecules. Thus, the performance of the dragline is preserved until a potentially catastrophic fall. *Argiope trifasciata* also spins silk with more consistent material properties when climbing vertically compared to dragline produced when crawling, which should increase the dependability of the total load a dragline could support when a spider falls (Garrido et al. 2002). Thus, spiders

can alter the performance of silk in anticipation of different functions, as also suggested by variation in the mechanical performance of major ampullate silk spun in different regions of cobwebs by *Parasteatoda tepidariorum* (Boutry & Blackledge 2009).

Despite the relatively simple function of silk lifelines, many questions remain. Any lifeline is only as strong as its attachment to the substrate, and draglines are secured via attachment disks produced from piriform silk glands (Coddington 1989). The morphology and chemical composition of attachment disks is beginning to be characterized, but almost nothing is known about their functional properties. One notable exception is the specialized attachment of the capture spiral to radii in orb webs, which can break thereby allowing the capture spiral to slide through them rather than breaking (Eberhard 1976). The piriform attachment disks for draglines are a mix of fibrous and gluey silks and contain spidroins that are unique to the piriform secretions (Blasingame et al. 2009; Perry et al. 2010). How attachment disks actually adhere to the substrate is still unknown.

5. ORB WEBS

The orb architecture is iconic among webs and evolved once in the ancestor of orbicularian spiders (Coddington 1982; Griswold et al. 1998; Blackledge et al. 2009b; Dimitrov et al. 2011). Orb webs played a critical role in the evolutionary diversification of spiders for at least two reasons. First, the development of the discrete aerial framework of major ampullate threads that support orb webs – the radii and frame threads – freed spiders from the constraints of terrestrial sheet webs, thereby acting as a “gateway” for the evolution of novel web architectures (Blackledge et al. 2009b). Equally important, though, is the implication of the mechanical function of the orb web in capturing flying insect prey for the evolution of silks themselves. Most prey-capture webs primarily extend the spider’s sensory environment and physically entangle arthropods, slowing the prey enough to facilitate capture by the web owner (Shear 1986). The targeting of flying insects by orb webs introduced two relatively novel selective pressures on silk: 1) dissipation of the massive kinetic energy imparted to orb webs when insects fly into them, and 2) the necessity for strong adhesion to prevent insects from falling out of orb webs.

5.1 Major ampullate silk.—Both the outer framework and supporting radii of orb webs are comprised primarily of silk from the major ampullate gland. Major ampullate silk evolved long before the orb web, ~375 mya (Ayoub & Hayashi 2009 in Garb et al. 2010), and is notably strong and tough even among basal lineages of spiders (Swanson et al. 2006). However, phylogenetic comparison shows that orb spiders’ major ampullate silk is significantly stronger and stiffer than other taxa, and this is hypothesized to reflect selection for the silk’s energy absorbing function in orb webs (Swanson et al. 2006). These changes in material properties correlate with the origin of a new protein, MaSp2, within orb spiders (Hinman & Lewis 1992; Gatesy et al. 2001). In contrast to MaSp1, whose repetitive elements are dominated by polyalanine and glycine-alanine motifs that fold the fibroins into β -sheets, MaSp2 contains a novel glycine-proline-glycine-glycine motif (Gatesy et al. 2001). The presence of the proline typically forces proteins into helical shapes that disrupt the formation of

β -sheets, and the tandemly arrayed motifs are hypothesized to fold into molecular “nanosprings” (Becker et al. 2003). This provides greater mobility within the amorphous region of the silk, thereby increasing toughness. The ratio of MaSp1 to MaSp2 expression correlates with at least some of the variation in mechanical performance of major ampullate silk among orb spiders (Liu et al. 2008; Elices et al. 2009).

5.2 Viscid adhesive silk.—The improved performance of dragline silk containing a blend of MaSp1 and MaSp2 spidroins correlates with the origin of orb webs per se at the base of the Orbiculariae. However, early orb weavers utilized a dry cribellate silk in capture threads that is still produced by Deinopoidea. Bouts of speciation instead correlate far more closely with the evolution of a new adhesive system in the viscid orb web, at the base of Araneioidea (Bond & Opell 1998). The evolution of viscid capture silk occurred early in the history of the orb web, and it is now utilized by 95% of all orb-weaving spiders (Bond & Opell 1998; Blackledge et al. 2009b). Viscid capture silk provides a major increase in the stickiness per volume of capture threads, which likely facilitates prey capture (Opell 1997). This in turn leads to higher growth rates and fecundity in araneoid vs. deinopoid orb weavers (Opell 1997).

Viscid silk achieves stickiness in a fundamentally different manner than cribellate silk. The basic differences are well documented in that cribellate capture threads rely upon physical entanglement and van der Waals interactions, while viscid glue is chemically adhesive (see review in Sahni et al. 2011a). However, a fundamental shift in the mechanics of both the axial threads and their adhesive silk also plays a critical role in adhesive performance. Cribellate capture threads are significantly stiffer and dissipate prey energy primarily through physical breaking of individual fibrils (Blackledge & Hayashi 2006b). Like most adhesive surfaces, cribellate silk resists detaching primarily along the edge of contact with a smooth substrate such as the wing of an insect. Thus, adhesive forces are determined not by the total area of contact but rather by the surface energy along the edge at which detachment occurs and the total number of cribellate fibrils (Opell 1994; Opell & Hendricks 2007).

Viscid capture threads overcome this constraint on adhesion through a highly effective suspension bridge mechanism that is enabled by the high elasticity of both the flagelliform axial fibers and the viscous glue droplets themselves (Opell & Hendricks 2007; Opell et al. 2008; Sahni et al. 2010). The viscid glue droplets have their own hierarchical structuring and consist of a core of cross-linked fibrous glycoproteins embedded in a liquid matrix (Opell & Hendricks 2010). Adhesion occurs mostly due to the interface of these glycoproteins with the surface (Vollrath & Tillinghast 1991). As a viscid thread begins to pull away from a surface, individual glue droplets extend greatly before they detach (Sahni et al. 2010; Opell et al. 2011). This allows multiple glue droplets to simultaneously resist pull-off, generating significantly more adhesion (Opell & Hendricks 2007). Furthermore, up to 50% of the total work required to pull a viscid thread free from a surface comes not from the glue, but instead from the extension of the axial fibers themselves (Sahni et al. 2010). The extensibility of both the glue droplets and the flagelliform silk is enabled by their hydrated states, which are maintained

Table 1.—Theoretical interactions between the material properties of silk proteins, the structures of silk threads, and the architectures of orb webs for each phase of prey capture. The number of pluses or minuses indicates the relative degree to which a particular trait influences a phase of prey capture. Parentheses indicate an influence that is largely indirect and due to the correlation between increased capture area and mesh width/fiber diameter. Note how several traits that positively influence stopping and retention potential have a negative influence on interception.

	Interception	Stopping	Retention
Material properties			
High toughness		+++	+
High extensibility		++	+++
High hysteresis		+++	+
Structural properties			
Thick fibers	–	+++	+
Large droplet size	–		+++
Architectural			
Large capture area	+++	(–)	+/(–)
Narrow mesh width	–	++	++

by a cocktail of hydrophilic salts in the glue droplets (Vollrath et al. 1990; Townley et al. 1991).

The dependence of viscid threads on water for their mechanical function has at least two important consequences. Adhesive forces are highly dependent upon the water content of the glue (Opell et al. 2011) and become optimized at intermediate humidity due to competing processes (Sahni et al. 2011b). Higher water content increases molecular mobility, and hence extensibility of both the axial threads and glue droplets, and facilitates spreading of the glycoproteins, but at the same time also begins to over-lubricate the contact surface. The precise humidity maximizing adhesion is determined at least in part by the salt content of the glues (Sahni et al. 2011b). Thus, variation in salt concentrations per se provides a very simple mechanism by which natural selection could act on silk adhesion, potentially leading to local adaptation to different web microhabitats. Unfortunately, comparative data are mostly lacking, although natural history observations show that the glues of some cyrtarachne spiders function only at extremely high humidity (Stowe 1986).

5.3 The function of silk in orb webs.—Although orb webs may play roles in courtship, thermoregulation and defense against predators, their primary function is to facilitate capture of flying insect prey. The role of orb webs in prey capture can be understood as a three-step process – intercepting, stopping and retaining prey until the insects are subdued by spiders (Blackledge et al. 2011). Success at each stage can be influenced by specific features of orb web architecture and silk mechanics, although general design principles are not always clear and functional tradeoffs are likely (e.g. Blackledge & Zevenbergen 2006; Blackledge & Eliason 2007). General discussion of web architecture and its influence on prey capture can be found elsewhere (Eberhard 1986; Nentwig Heimer 1987; Eberhard 1990; Zschokke 1999; Heiling Herberstein 2000; Blackledge et al. 2011), and Table 1 summarizes some of the significant factors affecting prey capture. In general, design features that facilitate the stopping and retention of prey are largely synergistic or neutral with

respect to one another. However, there are fundamental tradeoffs in how orb web design influences prey stopping and retention versus the initial interception of insects. Generally, spreading silk resources across larger webs with broadly spaced capture spirals should maximize the numbers of insects that fly through a web and contact silk. The most efficient design of an orb web that maximizes the number of prey contacting silk is constructed by spacing threads just larger than the average insect's wingspan (Eberhard 1986). Such a design is in general less visible to insects than more compact architectures, due to the thin diameters of silk threads and droplet sizes (Craig 1986; Craig 1988). However, these features reduce the probability of stopping and retaining prey once the insects are intercepted (Blackledge & Eliason 2007). Larger orb webs also increase the response time of spiders, since they need to navigate greater distances to entangled prey (see Nakata & Zschokke 2010; Zschokke & Nakata 2010 for discussion of spider response times).

A fundamental tradeoff between the interception potential and the stopping/retention potentials of orb webs is evident in comparisons of web architectures and silk mechanics among species. The dominant trend among orb spiders is associated with evolutionary shifts in body size (Sensenig et al. 2010). Larger species produce higher quality silk that is spun into orb webs with high stopping potential. Silk in these webs is packed relatively tightly, and there is a notable correlation in the improvement of the material properties of both major ampullate and flagelliform silk among larger species of spiders. One possible explanation for this pattern is the reliance on relatively large, but rare, insects demonstrated by Venner & Casas (2005) for *Zygiella x-notata* (Clerk 1757). The reliance on rare, large prey appears reasonably generalizable for orb spiders – a comparison of diverse spider species ranging more than 20 mm in maximum body length shows that roughly 85% of all biomass captured is composed of only a few insects proportionately similar in size to the spiders capturing them (Blackledge 2011). The kinetic energy of flying insects increases exponentially with their body size as both mass and flight speed increase. The ability of large species of spiders to target large insects depends more on how their web design facilitates the stopping and retention of difficult prey than on the probability of those prey encountering the web (Blackledge 2011). Unfortunately, the smallest orb webs, spun by the Mysmenioidea, are constructed using silk that is too thin to easily characterize using standard materials testing equipment, so nothing is known about the evolution of silk properties and web function in lineages evolving miniaturized body forms.

There is a close correlation between the numbers of rows of capture silk and the numbers of supporting radii in orb webs, with the ratio typically near one. There are two functional explanations proposed for this relationship. One hypothesis is that the constant ratio reflects a continuum between web architectures targeting high energy vs. low energy prey (Craig 1987). Here, species targeting higher energy prey package thicker silk threads more tightly into webs, while webs targeting lower energy prey contain fewer rows of widely spaced capture spiral supported by proportionally fewer radii. However, recent work suggests a compensatory tradeoff where better mechanical performance of silk in more “open”

webs – due both to improved material properties and thicker threads – results in stopping potential per unit area only slightly lower than webs with more tightly packed architectures for species of similar sizes (Sensenig et al. 2010). The second functional explanation does not involve prey capture per se, but instead reflects a constraint imposed by the very high compliance and relatively low tension of the capture spiral. More radii become necessary to hold the capture spiral in place as mesh width narrows to prevent adjacent capture threads from adhering to one another, thereby degrading web function. The absolute distance that a segment of capture spiral sags is proportional to its length (actually length cubed), so that shorter distances between radii in an orb web reduce the probability that capture silk segments can stretch and potentially entangle one another (see Rodríguez-Girones et al. 2010 for a similar discussion of how silk elasticity might constrain bridging thread length).

The retention time of insects in orb webs is typically quite short, often less than one second, providing little time for spiders to sense and subdue prey (Rypstra 1982; Blackledge & Zevenbergen 2006). The role of adhesive silks in prey retention is most investigated at the transition from cribellate to viscid capture silks (Opell 1997; Opell 1998; Opell 1999). Comparative studies have only recently begun within the viscid silk producing Araneoidea (e.g., Opell et al. 2008; Agnarsson & Blackledge 2009; Opell & Hendricks 2009). The total adhesive force generated by viscid capture threads scales remarkably closely with ~ 80% of breaking force for the underlying axial fibers, suggesting that the glue has evolved to safely detach from prey before the threads break, thereby maintaining the ability of the silk to re-adhere to struggling prey (Agnarsson & Blackledge 2009). Because of the close correlation between the tensile strength of capture spiral and radial silks (Sensenig et al. 2010), orb webs with high stopping potential should in general have higher retention potential, too. Relating inter-specific variability in thread stickiness to web function is difficult, however, because retention times vary so much among different taxa of insects, even when the insects are superficially similar in terms of body size or flight speed (Blackledge & Zevenbergen 2006). This variability is caused by differences in the flight and escape behaviors of insects, as well as the details of how cuticular features interact with adhesive silk (Opell & Schwend 2007). In general, variation in the average mesh widths of orb webs typically does not correlate closely with prey size (e.g., Nentwig 1983; Prokop 2006; but see Herberstein & Heiling 1998). However, some generalizations can be made about the effect of capture spiral spacing on prey retention from experiments altering the mesh width in webs by selectively cutting capture spiral rows. Narrow mesh width can increase retention times significantly for certain taxa of insects (Blackledge & Zevenbergen 2006), but it can also have surprisingly little effect on prey capture in the field. Blackledge & Eliason (2007) found that the weight gain of *Argiope aurantia* foraging in the field on webs with every other row of capture spiral removed did not differ in weight gain over the course of a single day compared to spiders on control webs. However, control spiders were significantly more likely to have larger prey wrapped in the web that they could continue to feed upon (Blackledge & Eliason 2007). This suggests that an important selective factor on the spacing

between rows of capture silk is not the ability of orb webs to retain average prey, but rather rare, large prey.

Finally, the mechanical interaction of orb webs with insect prey does not occur in isolation from other factors affecting prey capture. For instance, the microhabitat location of orb webs helps to determine prey availability and can influence the stopping potential of webs when insects “ricochet” among closely spaced webs (Uetz 1989; Rao 2009). The visibility of orb webs influences how effectively insects avoid webs and potentially their impact energy. The degree to which silk is visually attractive or repulsive to insects is remarkably controversial (see reviews in Herberstein et al. 2000; Blackledge et al. 2011). However, many features that improve stopping and retention potentials of webs, such as thicker, more tightly packed silk threads and larger glue droplets, clearly enhance web visibility, thereby potentially reducing the webs’ interception of insects (Table 1). Lastly, the attack behaviors of spiders vary greatly among taxa (Barrantes and Eberhard 2007) and are plastic (Robinson & Olazarri 1971), such that response time and running speed should vary with the sizes and retention potentials of orb webs (Zschokke et al. 2006; Nakata and Zschokke 2010). The degree to which web visibility and spider attack behaviors may coevolve with orb web mechanics is largely unknown.

5.4 Beyond orb webs.—The focus here is primarily on the function of silk in spider orb webs, yet orb webs are only a small fraction of all the silk structures produced by spiders, many of which function in unique but relatively unexplored ways. For instance, the sticky gumfooted threads in the cobwebs of theridiid spiders act as spring-loaded traps where energy is stored within the structure of the cobweb during prey capture (Argentean et al. 2006), rather than dissipated as in orb webs. The glue coating the gumfoot threads also differs in microstructure and adhesive response to humidity (Sahni et al. 2011b), as well as containing unique proteins (Hu et al. 2007). Unfortunately, nothing is known about the diversity of mechanical properties among the silk of different species of cobweb spiders, let alone anything about functional differences in their webs. The lack of knowledge is even more apparent when considering other types of prey capture webs, such as the many types of sheet webs produced by spiders, and non-prey capture structures such as egg sacs. Clearly there is a great need to expand research on both silk and webs “beyond the orb” (e.g. Eberhard 1990).

6. SUMMARY

Silk research is driven primarily by its biomimetic potential in industry and medicine (Hinman et al., 2000; Altman et al., 2003; Vollrath & Porter 2009), while research on spider webs is motivated primarily by the need to understand the ecology and evolution of these unique predators (Shear 1986; Wise 1993). Integrating these approaches is both advantageous and necessary (Harmer et al. 2011). Orb webs function in prey capture by first intercepting insects, then stopping their kinetic energy of flight, and finally retaining the insects long enough to be subdued by spiders. Each step in the process is determined by an interaction between the material properties of silk proteins, the structural properties of silk threads, and the architectures of webs. These interactions are largely synergistic for the stopping and retention potentials of webs,

but there is likely substantial conflict with respect to how silk structure and web architecture influence interception. Regardless, information on the material properties and structures of silk threads need to be better incorporated into future investigations of orb webs.

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